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Arturo Aguirre-Velarde, Fred Jean, Gérard Thouzeau, Jonathan Flye-Sainte-Marie. Effects of progressive hypoxia on oxygen uptake in juveniles of the Peruvian scallop, *Argopecten purpuratus* (Lamarck, 1819). *Aquaculture*, 2016, 451, pp.385-389. 10.1016/j.aquaculture.2015.07.030 . hal-01282771

HAL Id: hal-01282771

<https://hal.univ-brest.fr/hal-01282771>

Submitted on 4 Mar 2016

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Effects of progressive hypoxia on oxygen uptake in juveniles of the Peruvian scallop, *Argopecten purpuratus* (Lamarck, 1819)

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Abstract

A field survey performed in Paracas Bay (Peru), a major scallop culture area, showed that the Peruvian scallop, *Argopecten purpuratus*, periodically faces severe hypoxic events. Oxygen uptake rate (VO_2) of *A. purpuratus* juveniles facing progressive decrease of environmental oxygen saturation (from 100% to 5%) was measured at two contrasting temperatures ("normal condition" = 16°C and "warm condition" = 25°C). In normoxia, (oxygen saturation >70%) average VO_2 was significantly ($p < 0.001$) higher in warm condition ($0.20 \pm 0.004 \text{ mgO}_2 \text{ ind}^{-1} \text{ h}^{-1}$) than in normal condition ($0.12 \pm 0.007 \text{ mgO}_2 \text{ ind}^{-1} \text{ h}^{-1}$). The shape of the VO_2 response curve during increasing hypoxic conditions was evaluated using a segmented linear regression. The break points between linear segments allowed estimating the oxygen critical points (P_{cO_2} , oxygen saturation units), while the slopes of the various segments was used to assess the VO_2 regulatory capacity. In both temperature conditions at oxygen saturation lower than P_{cO_2} , VO_2 was a fourth of the values recorded in normoxic condition. This trend was more pronounced in the warm condition. Paradoxically, the estimated P_{cO_2} was lower in warm condition ($21.4\% \pm 0.7$) compared to the normal condition ($24.4\% \pm 1.9$). However, the study of the slopes at oxygen saturations higher than P_{cO_2} revealed that *A. purpuratus* can regulate its respiratory rate similarly and efficiently at both 16 and 25°C. Moreover, for VO_2 above P_{cO_2} , the estimated Q_{10} between normal and warm conditions was 1.78 (Arrhenius temperature = 4983 K), highlighting a moderate effect of temperature on VO_2 . These results reflect the adaptive capacity of this species to the changing environment along the Peruvian-Chilean coasts influenced by upwelling system and ENSO events. However, results from this study indicate that, at least during some periods, *A. purpuratus* spend more than 70% of its time exposed to hypoxic conditions below the estimated P_{cO_2} . Such conditions could have negative consequences on the species metabolism and harm the performance of *A. purpuratus* culture.

Keywords:

Argopecten purpuratus, Oxygen critical point, Oxyregulation, Respiration, Aquaculture, Peru

1. Introduction

Peruvian coastal waters are characterized by an intense upwelling system. The associated high primary production supports a large biomass of filter feeders (Thiel, 1978). Among those, the Peruvian scallop, *Argopecten purpuratus*, is a major species for Peruvian aquaculture. In 2012, aquaculture production in Peru reached more than 67 000 tons and a value of about 159 million USD (PRODUCE - Peru, 2015).

Massive mortality events, that affected production and subsequently local economy (Cabello et al., 2002; González-Hunt, 2010; Gonzales et al., 2012), have been repeatedly observed in coastal bays. Environmental monitoring (e.g. dissolved oxygen, temperature and toxic blooms surveys) is scarce in coastal areas in Peru.

Aquatic organisms can be characterized by their ability to regulate their oxygen uptake when exposed to moderate and/or severe hypoxia (Le Moullac et al., 2007). Species exhibiting an oxygen uptake dependent on environmental oxygen concentration are called "oxyconformers". In contrast, those who are able

to maintain their oxygen uptake independently of the external decrease in oxygen concentration, at least for a part of the oxygen decrease range, can be classified as "oxyregulators". Nevertheless, Mangum and Winkle (1973) stressed that this classification is no more than the two extreme ends of a range of gradual physiological responses. The oxygen critical point (P_{cO_2}) concept was introduced by Prosser (1973) to characterize the oxygen level below which an oxyregulator cannot keep its oxygen uptake independent of external concentration. The P_{cO_2} would coincide with the initiation of anaerobic metabolic pathways (Herreid, 1980; Pörtner and Grieshaber, 1993). Switching from aerobic to anaerobic energy production leads to a lower ATP yield per unit glucose and generates accumulation of end-products which might be metabolized when normoxic conditions resume. This phenomenon has been described as the oxygen debt (Herreid, 1980). Because metabolic pathways are affected by hypoxia, it can be hypothesized that energetics and subsequently growth and reproduction can also be affected.

Temperature also affects oxygen uptake regulation in marine bivalves by modifying P_{cO_2} and/or shape of respiratory response against progressive hypoxia (e.g. Le Moullac et al., 2007; Artigaud et al., 2014). In scallops bed of the Peruvian

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coast, water temperature variations up to 8°C in a few hours can be observed presumably due to variation in the intensity of the adjacent upwelling system (Aguirre-Velarde et al., 2014). In addition, Peruvian-Chilean coastal waters frequently experience important temperature variations due to El Niño Southern Oscillation (ENSO). The latter can induce dramatic increases of water temperature (about 10°C) (Wolff, 1987, 1988; Cantillán et al., 2007; Avendaño et al., 2008).

In order to better understand how physiology and energetics of *A. purpuratus* are affected by these fluctuating environmental conditions, this study was designed to focus on the metabolic response of this species to temperature and oxygen concentration. In this context, the present study aims at characterizing the respiratory response of *A. purpuratus* under progressive exposition to hypoxia at two contrasted temperatures (warm condition vs normal condition). A field survey was also performed in early 2013 in Paracas Bay, which is a main scallop culture area in Peru, to characterize the duration and magnitude of scallop exposure to hypoxic conditions.

2. Material and methods

2.1. Field monitoring

Field measurements of temperature and dissolved oxygen saturation of the near-bottom water (20 cm above the bottom) were performed in an *A. purpuratus* aquaculture bed located in Paracas Bay (Peru; 13°49'35" S, 76°17'43" W) using autonomous dataloggers (HOBO U22-001 and RBR TDO for temperature and oxygen, respectively) from January 1st, to March 10, 2013.

2.2. Laboratory experiment

Scallops ranging from 24 to 32mm in shell height were provided by La Arena hatchery (FONDEPES, Casma, Peru) and transferred to the Laboratorio de Investigaciones Acuicola of IMARPE (Callao, Peru) on the 27 of July 2013. After transfer to the laboratory, the scallops were acclimated into two thermoregulated 200-L tanks during 2 days with a constant 1µm-filtered seawater flow (8 L h⁻¹). No food was given during the whole experiment because (1) feeding rate is generally dependent on temperature and affects respiration rate and (2) the present experiment was performed over a short time period. One tank was maintained at 16°C ("normal condition") while the other one was progressively heated up to 25°C ("warm condition") in four days. Afterwards, the temperature was maintained constant.

Oxygen uptake measurements were performed in a third tank thermoregulated at the acclimation temperature (16 or 25 °C). Temperature recordings within the tanks (15-min intervals) showed that water thermoregulation for respiration measurements was accurate and stable. In the normal condition, the average temperature during the whole experiment was 16.0°C (max. = 16.2°C, min. = 15.9°C). In the warm condition, the average temperature during the experiment was 25.2°C (max. =

25.4°C, min. = 24.9°C). The experimental setting used was extensively described in Artigaud et al. (2014). Briefly, a computer-controlled system allowed to gradually decrease the concentration of oxygen within the experimental tank by the mean of injection of gaseous nitrogen (N₂) in the water. Gas exchanges with the atmosphere were limited by the mean of a floating PVC sheet placed on the water surface. The system allowed decreasing the dissolved oxygen percent saturation stepwise from 100% to 5% by steps of 10% to 5% every 2h. During the whole sequence of decrease of oxygen saturation, oxygen uptake rate by scallops was measured by repeated incubations in 0.59-L acrylic chambers. Six chambers were used in total, 5 chambers contained each four individuals, while the sixth one was used as a control and contained four empty scallop valves (which the external surface approximately equals the external surface of four individuals). Each incubation lasted 20 min; between two incubations, water within the chambers was automatically renewed by pumping water from the experimental tank for 5 min. At the end of each experimentation, scallop height and total volume were measured in each chamber.

For each temperature condition, the experimentation was repeated four times leading to a total of twenty replicates for each treatment. Between each experimentation, chambers were washed with a diluted hydrogen peroxide solution.

The individual oxygen uptake rate (VO_2 , mgO₂ ind⁻¹ h⁻¹), was calculated as:

$$VO_2 = \frac{O_2CR_{chamb} - O_2CR_{cont}}{n_{ind}}$$

with:

O_2CR_{chamb} : the oxygen consumption rate in chamber with scallops (mg O₂ L⁻¹ h⁻¹)

O_2CR_{cont} : the oxygen consumption rate in control chamber (mgO₂ L⁻¹ h⁻¹)

n_{ind} : the number of individuals into the chamber

Given the possible difference in scallop mean size between the chambers, estimated oxygen uptake rates were standardized to a 30-mm height individual using Bayne et al. (1987) formula:

$$VO_{2std} = VO_2 \cdot \left(\frac{H_{std}}{H_{mean}} \right)^b$$

with:

VO_{2std} : oxygen uptake (mgO₂ ind⁻¹ h⁻¹) standardized for an arbitrary height H_{std} (fixed to 30mm)

VO_2 : measured individual oxygen uptake into the chamber (mgO₂ ind⁻¹ h⁻¹)

H_{mean} : mean scallops height into the chamber (mm)

b : allometric relationship between size and oxygen uptake. In the review of Savina and Pouvreau (2004), the allometric coefficient that relates respiration rate to weight is close to 3/4 in bivalves. This coefficient was recalculated to 2.25 in this study in order to relate respiration rate to height (or length) based on the assumption that weight scales with cubic length (or height).

The oxygen critical point (abrupt decrease in respiration rate or break point) was calculated using a segmented linear regression method (Muggeo, 2003), as proposed by Artigaud et al. (2014), from measurements of oxygen uptake vs oxygen saturation. The capacity of oxygen uptake regulation under progressive hypoxia was evaluated through the "O₂ regulation percentage" of Hicks and McMahon (2002). This value corresponds to the ratio between (1) the area beneath the curve of oxygen uptake versus oxygen saturation (expressed as percentage of maximum oxygen uptake i.e saturation = 100%) and (2) the area achieved by a perfect oxyregulator (displaying a constant respiration rate whatever the level of oxygen saturation). All computations were performed using R software (R Development Core Team, 2011); segmented linear regressions were performed using the "segmented" R package (Muggeo, 2008).

The effect of temperature on *A. purpuratus* oxygen uptake was assessed through the Q_{10} temperature coefficient calculated as: $Q_{10} = (\bar{k}_1/\bar{k}_2)^{10/(T_2-T_1)}$, where \bar{k}_1 is the metabolic rate measured at temperature T_1 , \bar{k}_2 is the metabolic rate measured at temperature T_2 , and $T_1 < T_2$ using respiration rates in normoxia (VO_{2std} for oxygen saturation above 70%). The Arrhenius temperature (T_A , K) is frequently used to assess the effect of temperature on physiological rates in bioenergetic models within the thermal range tolerance of a species (Kooijman, 2010). This parameter was estimated from Q_{10} using the relationship proposed by Kooijman (2010): $T_A = [\ln Q_{10} \cdot T \cdot (T + 10)]/10$, with T the reference temperature (i.e. 289 K)

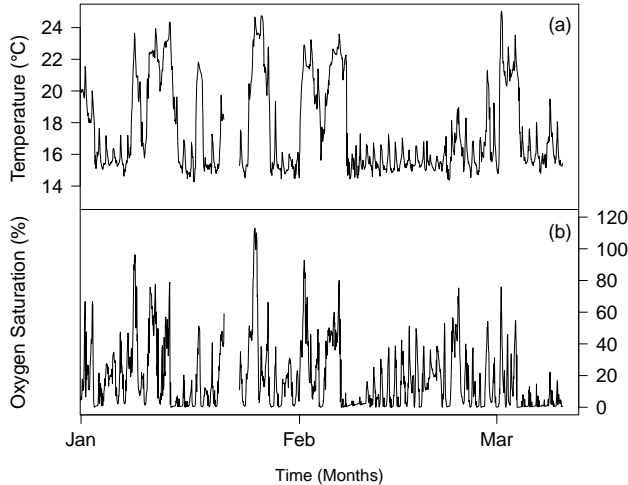


Figure 1: Temperature and oxygen saturation of near-bottom water (20 cm above the bottom) of an *A. purpuratus* aquaculture bed located in Paracas Bay (Peru, 13°49'35" S, 76°17'43" W) measured between the January 1st, and the March 10, 2013.

3. Results

During the monitoring period, the oxygen saturation of the near bottom water varied from 0% to 112% (Fig. 1) and the average saturation was 18%. During the 69 days of monitoring, the aquaculture bed faced under saturation below 24% for 70%

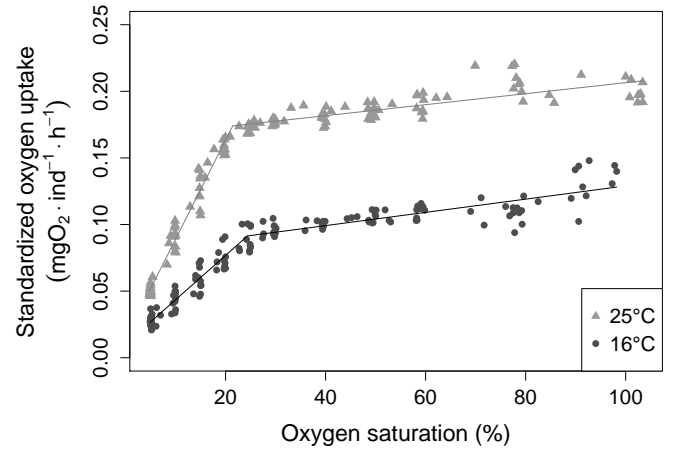


Figure 2: Standardized (30mm shell height) individual oxygen uptake rate of *Argopecten purpuratus* facing progressive hypoxia at 16 and 25°C. Lines are the segmented linear models used to calculate the critical oxygen point at both temperatures. Estimated break points (P_{cO_2}) were 24.4% (CI=1.9) at 16°C and 21.4% (CI=0.7) at 25°C. No significant difference in the slopes of the linear segments above P_{cO_2} was found between the two treatments, whereas slopes were significantly different for oxygen saturation below P_{cO_2} .

of the time. Temperature varied between 14.2°C and 23.7°C and average was 16.3°C. Dramatic daily temperature changes were frequently observed: on March 1st 2013 the temperature varied from 14.7°C to 22.9°C (increase of 8.2°C) within a few hours.

Measured standardized oxygen uptake rate in normoxic conditions (O₂ saturation >70%) was $0.12 \pm 0.007 \text{ mgO}_2 \text{ ind}^{-1} \text{ h}^{-1}$ at 16°C and $0.20 \pm 0.004 \text{ mgO}_2 \text{ ind}^{-1} \text{ h}^{-1}$ at 25°C. Those data allowed to estimate the Q_{10} to 1.78 and the corresponding value of T_A was 4983 K. Under severe hypoxia (O₂ saturation close to 5.5%), VO_{2std} was $0.027 \pm 0.002 \text{ mgO}_2 \text{ ind}^{-1} \text{ h}^{-1}$ at 16°C and 0.050 ± 0.002 at 25°C, that is 22.5% and 25% of the values measured in normoxic conditions, respectively. In both normoxic and severe hypoxic conditions, VO_{2std} was significantly higher in warm than in normal condition ($p < 0.001$, Kruskal Wallis test).

The results of the segmented linear regression models fitted on the oxygen uptake rates as a function of oxygen saturation indicate a P_{cO_2} (break point) at $24.4\% \pm 1.9$ in normal condition (16°C) and at $21.4\% \pm 0.7$ in warm condition (25°C) (Fig. 2, tab. 1). In both conditions, a strong decrease of oxygen uptake rate is observed when oxygen saturation drops below the P_{cO_2} (break point), segmented linear regressions indicating significant changes in the slopes of linear segments (Davies' test, $p < 0.001$). Likewise in both experimental temperature conditions, the regression slopes show that both P_{cO_2} lower and higher segments depend significantly ($p < 0.001$) on oxygen saturation although in a different extent.

Comparison of the slopes of the segments above and below the P_{cO_2} was assessed through analysis of covariance (ANCOVA); it allowed comparing the respiratory response of the scallops to progressive hypoxia between two temperature expo-

Table 1: Oxygen critical points values (P_{cO_2}) and percentage of regulation estimated for *Argopecten purpuratus* at 16 and 25°C using segmented linear regression. The table indicates the slopes and confidence intervals of the linear segments below and above the break points (P_{cO_2}).

Temperature (°C)	P_{cO_2} (% \pm CI)	Linear segment slopes		% Regulation (%)
		Segment < P_{cO_2}	Segment > P_{cO_2}	
16	24.4 \pm 1.9	3.34 $10^{-3} \pm 3.3 \cdot 10^{-4}$	4.97 $10^{-3} \pm 7.6 \cdot 10^{-5}$	74
25	21.4 \pm 0.7	7.44 $10^{-3} \pm 3.4 \cdot 10^{-4}$	4.13 $10^{-3} \pm 6.7 \cdot 10^{-5}$	82

tures. The comparison of the segments superior to P_{cO_2} shows no significant interaction ($p > 0.05$) between temperature and oxygen saturation on oxygen uptake indicating no significant difference for slopes between the two temperature conditions. Thus for saturations above P_{cO_2} , regulation of oxygen uptake in function of oxygen availability is identical. For saturations below P_{cO_2} , interaction between temperature and oxygen saturation was significant ($p < 0.001$) indicating that the slopes are significantly different between treatments. Therefore, below P_{cO_2} , the oxygen uptake regulation depends on oxygen saturation but also on temperature. At 25°C, respiration rate decrease is 2.2-fold higher than at 16°C when saturation falls below P_{cO_2} . Finally, regulation capacity was slightly higher at 25°C (82%) than at 16°C (74%; see Table 1).

4. Discussion

Traditional dichotomy between “oxyconformers” and “oxy-regulators” has been criticized because of the varied responses of organisms facing progressive decrease of environmental oxygen saturation (Mangum and Winkle, 1973; Taylor and Brand, 1975). Herreid (1980) considers that “good regulators” have low P_{cO_2} values and abrupt transitions and steep conformity slopes. “Poor regulators” are expected to have a more gradual transition from regulation to conformity. Bivalves species inhabiting periodically hypoxic habitats, are generally found to be better regulators when submitted to progressive hypoxia (Griffiths and Griffiths, 1987). This is the case in Peruvian coastal bays where the environmental monitoring presented in this study showed that *A. purpuratus* is frequently exposed to severe hypoxic conditions. The effects of environmental hypoxic events on marine natural (Llanso, 1992) or cultured (Brokordt et al., 2013) populations depend on the intensity and duration of these events. Brokordt et al. (2013) found that hypoxia exposition affects the escape capacity of *A. purpuratus* increasing vulnerability to predation and decreasing physiological capabilities to support other stress factors. To maintain oxygen uptake when oxygen availability decreases, bivalves can respond by increasing water pumping/ventilation (Tran et al., 2000) and cardiac activities (Grieshaber et al., 1994). This set of responses can be considered as a “oxyregulation effort”, where P_{cO_2} represents the limit of regulatory ability (Grieshaber et al., 1988). Although oxygen uptake is not completely independent of oxygen saturation for oxygen saturations higher than P_{cO_2} (“regulated segment”), *A. purpuratus* exhibits relatively low P_{cO_2} (Fig. 2) and can thus be considered as a good

regulator. Recently, Artigaud et al. (2014) estimated a similar P_{cO_2} value (23.8% at 18°C) for *Pecten maximus* which is phylogenetically closely related. It can thus be hypothesized that morphology/anatomy plays a role in the physical oxyregulation ability (e.g. ventilation, oxygen perfusion). Nevertheless, results of Artigaud et al. (2014) indicate that in *P. maximus*, which is less naturally exposed to abrupt changes in temperature, regulation ability is more sensitive to temperature.

Generally, P_{cO_2} increases with temperature (Herreid, 1980), this relationship resting upon the temperature-dependence of oxygen solubility in seawater (Le Moullac et al., 2007). Interestingly, the difference of estimated P_{cO_2} was very low between both temperature exposures in this study, and was associated with a regulation ability slightly higher at 25°C than at 16°C. This pattern might be associated with an increased metabolic capacity for ciliary ventilation and/or hemolymph perfusion of the gills (Alexander and McMahon, 2004). This can explain also the significantly higher oxygen uptake in warm conditions under severe hypoxia (O_2 saturation near 5.5%) compared to normal (16°C) condition. Such a positive relationship between temperature and oxygen uptake regulation has also been found in the fresh water bivalves *Sphaerium simile* (Waite and Neufeld, 1977) and *Dreissena polymorpha* (Alexander and McMahon, 2004). On the other hand, in upwelling zones, as along the Peruvian coast, hypoxia can occur at low temperatures. Under low temperature conditions, the reduced efficiency of regulation strategies may cause a early decrease of oxyregulation effort and consequently of oxygen uptake rate. Increased metabolic rate (higher energetic demand) at elevated temperatures may need extending oxyregulation effort to maintain aerobic metabolism. Indeed, the latter is more efficient in terms of ATP production.

Respiration rates generally increase with body temperature until a threshold temperature is reached (Hand and Hardewig, 1996). The Q_{10} value of 1.78 calculated from oxygen uptake data in normoxia is close to values characteristic of temperature-dependent physiological response (Q_{10} ranging between 2 and 3; Willmer et al., 2005). This Q_{10} value is slightly lower than the lower limit of this range, which reflects a moderate effect of temperature on physiological rate. The latter may favor the maintenance of homeostasis in an environment presenting high temperature fluctuations. Comparisons of subtidal (relatively stable temperature) and intertidal (highly fluctuating temperature) mollusk species show that species experiencing high temperature fluctuations (intertidal) present lower Q_{10} (e.g. Sokolova and Pörtner, 2003; Dunphy et al., 2006). A.

purpuratus displays a ability to adapt/acclimate to both high temperature, i.e. during El Niño events ($\approx 24^{\circ}\text{C}$ in Peru, Wolff, 1987), and low temperatures ($\approx 12^{\circ}\text{C}$ in Southern Chile, Gonzalez et al., 2002; $13\text{--}14^{\circ}\text{C}$ in Northern Chile during la Niña events, Cantillán et al., 2007). In addition, similarly to intertidal species, temperature changes higher than 8°C , combined with dramatic changes in oxygen concentration, were recorded in few hours in Paracas Bay, Peru. Wolff (1987) suggested that *A. purpuratus* was a relict form of the subtropical fauna which once inhabited Chile and Peru during Miocene. Adaptations to warm conditions, including hypoxia handling, may have preserved after the general cooling of the oceans at the end of the Miocene due to periodical El Niño occurrence on the Peruvian coastal zones. This relative low effect of temperature on physiological rates combined with a good regulation of oxygen uptake under hypoxia might explain the ability of this species to adapt/acclimate to such conditions. In an environment where trophic resource is poorly limiting, *A. purpuratus* is well adapted to cope with temperature changes and to deal with frequent hypoxia events under both cold and warm conditions. Such a strategy would allow maintaining aerobic metabolic pathways and efficiently using food resources (e.g. for growth and reproduction) under low oxygen concentration. The success of *A. purpuratus* aquaculture can be related to its ability to acclimate to this very dynamic environment, while displaying important growth rates in comparison to other scallops species. It is clear from this study however that *A. purpuratus* aquaculture could be optimized by selecting culture areas (bottom and suspended cultures) presenting the best fit between temperature and oxygen fluctuations, and metabolic rates.

Several studies showed that temperature strongly impacts the organisms ability to cope with hypoxia (Newell, 1978; McMahon and Wilson, 1981; Hicks and McMahon, 2002; Jansen et al., 2009; Alexander and McMahon, 2004; Le Moullac et al., 2007; Pörtner, 2012; Artigaud et al., 2014). Artigaud et al. (2014) found an inverse relationship between the temperature and percentage of regulation in *P. maximus*, while Hicks and McMahon (2002) found a direct relationship in *Perna perna*. In the present study, the calculated percentage of regulation was slightly greater at 25°C than at 16°C . However, two phases can be considered in the response to hypoxia: a highly regulated segment (above P_{cO_2}) and a poorly regulated segment (below P_{cO_2}). The slopes of the highly regulated segments seems as a pertinent criteria to assess oxyregulation ability. This study showed close P_{cO_2} values (21.4 and 24.4%) and no significant difference in the slopes of the highly regulated segments between the two temperature conditions. The combination of these two observations indicates that *A. purpuratus* oxyregulation ability is only slightly affected by temperature. This physiological acclimation ability displayed between these two widely remote temperatures may be linked to an adaptive response to a highly variable environment in terms of temperature and oxygen concentration (e.g. ENSO and high frequency events) and may contribute to explain the wide geographical distribution range displayed by this species.

In the poorly regulated segments, the decrease of oxygen uptake is more abrupt at 25°C than at 16°C (Fig. 2). This differ-

ence can be explained by the higher metabolic rate observed at 25°C (that might include oxyregulation effort), causing a more pronounced energetic decrease when oxygen saturation drops near zero. The inability to maintain the oxygen consumption rate below the P_{cO_2} marks the beginning of energetic anaerobic pathways (Grieshaber et al., 1988; Pörtner and Grieshaber, 1993). While many bivalves are adapted to survive periodic hypoxia (Le Moullac et al., 2007), less efficient energy production under anaerobic conditions can affect their energetics. The synthesis of endproducts to be metabolized when normoxic conditions resume can generate oxygen debt (Herreid, 1980). Chronic exposure to severe and prolonged hypoxic conditions, as in the Peruvian coastal waters, might affect the *A. purpuratus* energy budget by reducing the energy available for the major metabolic functions, thus affecting growth, reproduction and immune response with consequences for culture performances.

5. Conclusion

The Peruvian-Chilean coastal marine area presents an environment highly variable in terms of temperature and oxygen saturation. The results of this study highlight *A. purpuratus* ability to efficiently regulate its oxygen uptake in a wide temperature range. The observed low oxygen critical points indicate an important regulation capacity of oxygen uptake at both normal and warm conditions. Although oxyregulation decreases considerably for oxygen saturations lower than the critical point, the oxygen uptake under severe hypoxic conditions is not null. The ability of *A. purpuratus* to deal with oxygen limiting conditions might provide an adaptive advantage to acclimate to environmental conditions along its distribution range. Further studies must focus on the anaerobic metabolic capacity and the effect of hypoxia on the energy balance of this scallop species.

Acknowledgments

We thank the Instituto del Mar del Peru and especially Carla Aguilar for allowing the use of the IMARPE experimental facilities. We thank "Los Chichos" Diego Herrera and Alex Vega for their active help during the experiments. We thank also the Hatchery of "La Arena" (FONDEPES) for providing the scallops used in this experiment. This work is part of a PhD thesis supported by IRD within the framework of the LMI DISCOH, and LabexMER (ANR-10-LABX-19-01).

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